Art. VIII.—*The Temperatures of Reptiles, Monotremes and Marsupials.*

(Plate VI.).

By Alexander Sutherland.

[Read 4th June, 1896.]

There has for many years past been a tendency to diminish or ignore the distinction between the cold-blooded and the warm-blooded types of animal life. Quite a number of writers adopt the habit of speaking of "the so-called cold-blooded animals," as if the contrast were an unfounded belief that increasing knowledge is fast abolishing. Yet the difference is one that is not only real, but in some respects radical. In very few, however, of nature's classes is there found a line of sharp demarcation, and the chief purpose of this paper is to point out that, though the distinction between the two types is real, there lies between these two types a line of steady gradation.

Although the invertebrates have the capacity of producing heat, they are themselves cold-blooded. With the exception of the insects, they very rarely rise more than a fraction of a degree above the temperature of the media in which they happen to be. According to observations of Professor Valentin, polypi, medusæ, echinoderms, molluscs, crustaceans and cephalopods are able to raise themselves about a fifth of a degree, sometimes as much as three-fifths of a degree, above their environment.*

Among insects the power of heat-production is very much greater. Though essentially cold-blooded creatures, in the sense that they have no fixed standard of body-heat towards which they approximate, they are almost always warmer than their media; but if they are at rest that excess is only a degree or two. In case, however, of severe exertion, they are capable of warming themselves to a remarkable extent. George Newport showed that an ants', bees', or wasps' nest at a period when its inmates are dormant will not be more than a tenth of a degree warmer than the surrounding air. But when the insects are roused and excited they are able, by rapid movements of their wings, to warm

* All Degrees in this paper are Centigrade.

themselves and their nests very considerably. As the result of twelve experiments on a nest of thirty bees, Newport found an average elevation of 3·5°; but on seven occasions when he violently agitated them he obtained an average elevation of 5·3°. At times when bees are naturally much excited, as at swarming time, their temperature may rise as much as 22°. According to experiments of Juch and Newport (Phil. Trans., 1837, p. 259), ants in an ordinary state of activity keep their nests some seven or eight degrees warmer than the surrounding air, but when agitated the difference readily rises to twelve or thirteen degrees.

These more intelligent insects apparently make use of this capacity of generating heat for the purpose of quickening the hatching of eggs and the development of nymphs. Nevertheless they are distinctly cold-blooded animals, for at rest they take the temperature of their media, and any elevation is temporary and due to the immediately preceding display of energy.

In the case of fish, amphibia and reptiles the same is true. At rest all of them remain at the temperature of their environment, rising and falling with it. and showing no capacity, however rudimentary, of maintaining a fixed and characteristic temperature; yet all can warm themselves by exertion. The large blue-tongued lizard, which is common in the southern parts of Victoria (*Cyclodus gigas*), can warm himself as much as half a degree in ten minutes of anger. In five experiments of this sort I found that different individuals had different capacities of being irritated, but the average was a trifle under half a degree for ten minutes of exasperation.

By activity, and consequent heat-production, all fish, amphibia and reptiles seem able to keep themselves a little warmer than the air or water in which they dwell. Dutroche tells us (Ann. des Sciences Nat., xiii., p. 20) that the newt can keep itself from 2° to 5½° above the temperature of its medium, the turtle 1½° to 3½°, and the common green lizard of France (*Lacerta viridis*) from 4° to 7°. Max Furbinger asserts that species of blind-worm rise as much as 8° above the temperature of the air. Fish at rest appear to take almost absolutely the temperature of the water wherein they live, but after a struggle, or any other form of energy, they may warm themselves two or three degrees.

This, however, has no real affinity with a warm-blooded habit. And yet these creatures approach in a remote way the warm-blooded condition by sometimes developing a capacity for heat-production in the action of their viscera. Dumeril has shown that snakes by mere digestion can warm themselves from 2° to 4°, the maximum temperature occurring about twenty-four hours after a meal. Moulting may warm a snake nearly a degree, and frogs, lizards and serpents all warm up with amatory emotion.

Thus it constantly happens that these animals, though essentially cold-blooded, may be observed at temperatures somewhat above that of their environment. But in general that excess is not great, and it leaves the distinction between the warm-blooded and the cold-blooded type quite unaffected.

The true criterion of the difference is of course the concomitance of the temperature of the animal and its medium. An animal of the warm-blooded type may vary a trifle in its general body temperature when the climate alters, but it maintains an almost constant degree of heat. The reptile, though it may maintain itself a few degrees above the surrounding temperature, always varies with it, rising and falling so as to keep always the same number of degrees in excess.

In two experiments I conducted to see how far this concomitancy held, I placed two specimens of the large lizard already mentioned into a small tank of water, so that only their noses were above water. I then warmed up the water at various rates of speed by means of one or more lamps. The following tables will show how closely the lizards followed the temperature of the enclosing water :—

Lizards, Average Weight, 350 Grams.

Time.	Temp. of Water. C.	Temp. of Lizard. C.	Time.	Temp. of Water. C.	Temp. of Lizard. C.
2·30	18·4	18·0	4·15	25·2	24·1
2·45	19·8	18·9	4·30	26·0	24·7
3·0	20·6	19·9	6·15	29·2	28·9
3·15	21·8	20 7	8·0	32·8	31·4
3·30	22·8	21·7	9 0	31·0	29·4
3·45	23·1	22·5	11·0	24·0	23·5
4·0	24·4	22·9			

LIZARDS, AVERAGE WEIGHT, 330 GRAMS.

Time.		Temp. of Water. C.		Temp. of Lizard. C.	Time.		Temp. of Water. C.		Temp. of Lizard. C.
4·20	...	11·5	...	12·0	5·10	...	21·0	...	19·5
4·25	...	14·4	...	13·6	5·15	...	21·6	...	19·8
4·30	...	16·0	...	14·6	5·20	...	22·4	...	20·4
4·35	...	16·7	...	15·2	5·25	...	23·0	...	20·9
4·40	...	17·2	...	16·0	5·30	...	23·6	...	21·4
4·45	...	17·8	...	16·8	5·40	...	24·6	...	22·1
4·50	...	18·3	...	17·0	7·0	...	30·1	...	28·6
4·55	...	19 0	...	17·8	8·0	...	35·0	...	33·6
5·0	...	19·6	...	18·2	9·30	...	29·5	...	28·0
5·5	...	20·2	...	19·2	11·0	...	24·0	...	23·0

Similar tables might be made out for fish, for turtles, for snakes, and all the cold-blooded animals, showing that they take their temperature absolutely from the media in which they exist, and when it is found that they do not exactly coincide with it, the cause is generally to be found in the fact that for a rising or falling temperature of the medium the animal will not at once respond to the change; it lags behind and will in a cooling medium be warmer, in a warming medium cooler than its surroundings. Occasionally, however, a slight excess of heat is due to the animal's activity.

Cyclodus gigas is a very sluggish creature, and if left alone never warms himself by any exertion, yet if one takes his temperature in the early part of the day it will almost always be found to be below that of the air. After sunset, it is generally higher. During two years I kept specimens of this species in a box, sometimes six or eight, sometimes only two or three. I took their temperatures morning and evening, not altogether continuously, but throughout the larger portion of that time. The average of all these observations gave for lizards 18·1°, for the air 18·4°. This is a very close approximation considering that the temperatures had the wide range that lies between 12° and 32°. The lizards appear to be colder a little than the air. This I believe to be due only to the fact that, taking temperatures before eight o'clock in the morning, the lizards were still considerably in the rear of the air temperature, while between five and six o'clock in the evening, though they were above the air temperature, the excess then did not wholly balance the morning deficiency.

I am convinced that if one took the temperature of a quiet lizard every hour for a month, the average would correspond almost exactly with the average temperature of the air. The morning and evening observations which I took would give a less exact result, though from them the difference is only three-tenths of a degree.

A cold-blooded animal is therefore one which when at rest takes its temperature almost absolutely from its environment. When a snake is asleep, the slow beat of its heart, eight or ten times in a minute, will generally, so far as I have noticed, keep the muscles of the heart itself about six or eight tenths of a degree warmer than the rest of the body. This, diffused through the whole body, must have a tendency to slightly increase its temperature, but only to a minute extent. The same snake, however, after a time of activity may be two or three degrees above the heat of the surrounding air. Yet even that is inconsiderable compared with the extreme rise and fall of the creature's temperature with the alternations of day and night, of hot or cold weather.

The steps whereby the more active and intelligent warm-blooded types have arisen from this lethargic level would form a fascinating subject for enquiry, but I purpose here only the much easier and more prosaic one of recording that such steps, however caused, do actually present themselves, and that these are in the most perfect accordance with the existing classification, which is based on anatomical considerations alone.

The monotremes are, in consideration solely of their more reptilian anatomy, placed lowest in the scale of mammals. Their low temperature would entirely justify, were justification in any way needed, the position thus assigned them next to the reptiles. The temperature of the duck-billed platypus has been determined by Baron Miklouho-Maclay to be, as the average of three observations, 24·8° when the water in which the animals were kept averaged 22·2°. (Journ. of Linnæan Soc. of N.S.W., VIII., p. 425, and IX., 1204.)

Now, the average of forty-five specimens of the ten higher orders of the mammalia, excluding the monotremes and marsupials, is

38·9°, as calculated from Dr. John Davy's lists (Edin. Phil. Journ. 1825, p. 300), while the average of a similar but shorter list supplied by Max Fürbinger is 39°. We may take this as fairly indicative of the general mammal temperature, which does not, except in constitutional disturbances, vary so much as two degrees on either side of this limit. No mammal indeed seems in good health to be warmer than 40°; scarcely any descend lower than 37°.

The platypus, therefore, at only 24·8° is almost a cold-blooded animal. The only other genus of monotremes, the echidna, carries us a step upwards. Baron Miklouho-Maclay's average of five observations is 28°, while the air was 20°. I have kept at different times fourteen specimens of *Echidna hystrix* and made twenty-seven observations on the temperatures of all I happened to have at any particular time. I found the average to be 29·4°, or nearly a degree and a half above that of the Baron. But these animals show their affinity with the reptiles by a temperature so variable with the weather that we may readily expect the average of one series of experiments to differ very considerably from that of another.

An echidna one cold morning was so low as 22°; another, brought in from the forest in a sack exposed to a fierce midday heat, registered so high as 36·6°. The following table will represent the general character of the variations, the temperatures in each case being the average of from three to six individuals, which never varied from one another at the same time more than a fifth of a degree :—

Echidna.		Air.	Echidna.		Air.
22°	...	14·4°	29°	...	25°
27·5°	...	14°	29·5°	...	22·2°
27·7°	...	14°	29·5°	...	24°
27·7°	...	18°	30·3°	...	18°
28·2°	...	19°	31·1°	...	23·3°
28·3°	...	16·6°	31·4°	...	22·4°
28·7°	...	16°	32·2°	...	31·2°
29°	...	22·7°	32·9°	...	18·6°
29°	...	23°	36·6°	...	45°

This is an immense range for a mammal, and suggests a reptilian want of capacity for temperature regulation. Moreover, though the concomitancy between the air and the body temperatures is by no means strict, there is enough to show that the one in a large measure follows the other. It is to be remembered that while a monotreme may rise and fall with the air, yet the one change will follow the other after a definite period of time, and an hour after sunset, though the air in a box may have grown much cooler, the echidnæ in that box may have only begun to cool.

The temperatures given by Dr. Richard Semon in the recent number of his important work, *Forschungsreisen in Australien*, run as follows:—

Echidna.		Air.	Echidna.		Air.
26·5°	...	21·5°	31·5°	...	18°
29·5°	...	22°	34°	...	31·5°
30·5°	...	18°	34·2°	...	22·5°
31°	...	24°			

Here also the generally low temperature, combined with the wide range, even though it is not strictly concomitant with changes in air-temperatures, seems to suggest affinities with reptiles.

The next stage in the anatomical classification brings us into the order of the marsupials, and here again we make an upward step in view of a temperature higher, but not so high as that of mammals in general; steadier, but not so steady as is usual in all the remaining orders. I have observed the temperatures of sixteen different species of marsupials, and they average 36° exactly, as the result of 126 observations. They are thus 3° below the average of other mammals.

The marsupial whose temperature, so far as I have observed, comes next above the monotremes is the wombat, which stands at 34·1°, as the average of single observations made on two specimens (*Phascolomys lasiorhinus*, 34·3°, and *P. platyrhinus*, 34°). Next seems to stand the genus Petaurus, or flying squirrel. Mr. Ernest Le Souëf was good enough to observe for me the temperatures of five specimens in the Zoological Gardens of Melbourne. The average is 35·7°.

After that comes the genus Phascolarctos, our little native bears or koalas. I have kept numerous specimens of this animal (*P. cinereus*) on his native gum trees, with nothing artificial about him save a strap and rope whereby he could be pulled down from time to time to have his temperature observed. Thus I made eighty-three observations, the average of which amounts to 36·4°. Females at the breeding time are always very decidedly above the ordinary degree of warmth. If such cases be excluded, the average is exactly 36°. But the average for males alone is only 35·2°. The range of variation may be seen in the following nine observations taken at intervals upon the same female :—

Koala.		Air.	Koala.		Air.
35·0	...	7·7	36·0	...	13·1
35·2	...	11·5	36·1	...	22·0
35·6	...	10·0	36·5	...	24·5
35·7	...	19·0	36·8	...	16·0
36·0	...	22·0			

The range is here seen to be not very wide, yet I have often known healthy specimens that had been for a while in the sun stand as high as 37·9°, while on a cool day or in a very shady place the same individuals would be only 35·3°, a range greater than we would find under the same circumstances in any of the higher mammals. The highest register I ever obtained for a thoroughly healthy koala was 38·4°, which is a degree and a half above the normal temperature of man; the lowest was 34·9°, or nearly two degrees below man's normal. The former temperature would in man imply some constitutional derangement, a distinct case of feverishness; in the koala it denotes only that it has been out in the sun. The lower temperature, though common in the koala, is never met with in man except in rare pathological conditions. It is below the range of our ordinary clinical thermometers.

I found that a big male specimen of this species, kept in a cool shady place and registering 34·9°, could, by being brought into a bright sun, be raised a tenth of a degree for every five minutes he was kept in it. I regret that when I had abundant opportunities I did not determine how far this warming process would go; but I have seen it continue for more than two hours at a time.

Females were, with only one exception, of higher temperature than males when under the same conditions; and the divergence was always greatest when the females were suckling their young, the average of twenty-five observations giving an excess of 1·2°. The koala has only one young one at a time, but she has two teats, one on each side of her pouch; of these only one would be functional at a time. That side of the pouch whereon was the functional teat was invaribly warmer than the other. The average of twenty-six observations gave 36·6° for the one side as against 36° for the other.

According to observations taken for me by Mr. Ernest Le Souëf the Dasyures come next at an average of 36°.

Phalangers stand next in order. The average of twenty two observations on from two to four specimens of the ring-tailed opossums (Phalangista) gave 36·6°, which is only a little below the normal human temperature. But again the range was much greater than one finds in any of the higher mammals. In cool weather, with the thermometer at 16·8°, a male would register about 35°, a female about one-tenth of a degree higher; but in warmer weather, though still in the shade, where the thermometer registered 31° to 35°, the opossums would be about 37°; I once observed two of them, the only ones I then had, for nearly a fortnight together, which averaged about 39°, but as they died soon after, I fear they had not been in good health when these records were made.

Mr. Ernest Le Souëf took for me the temperatures of three of these Australian opossums in the Melbourne Zoological Gardens. *Phalangista vulpina* gave 36·1°, *Phalangista fuliginosa* 37·3°. This corresponds with Selenka's observations of the true opossums (Didelphys), which ranged about 37°.

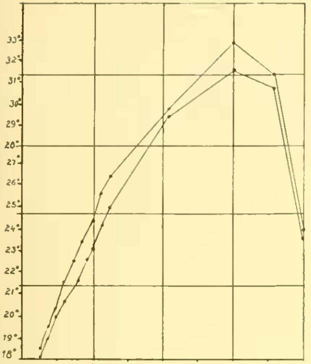
I have made only four observations on the temperatures of the kangaroo family. They are a little under the human standard. *Macropus giganteus* gave 36·6°, *Halmaturus bennettii* gave 37·1°, *Petrogale xanthopus* 35·9°, while the tree kangaroo (*Dendrogalus grayi*) was exactly at the human standard, 37°.

From the few recorded temperatures of rodents and insectivores, I should think it most probable that they came next in order, with perhaps the cetacea and sirenia, judging from occasional records, as almost on the same level. All the other orders of mammalia stand uniformly much above the human temperature.

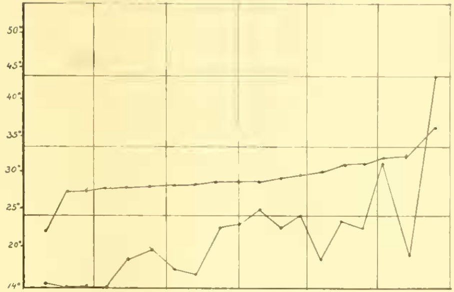
It is clear, therefore, that there are grades of temperature, and that the mammals which are classed lowest on anatomical grounds are not only of the lowest temperature, but also of the greatest range, and they are likewise, of all mammals, those which are under the strongest and most direct influence of the temperature of the environment.

Similar, though much less complete connecting links may be seen in the case of birds. The lowest of birds are the Ratitæ, or Cursores, and these appear to have the lowest temperature. Mr. Ernest Le Souëf, with an amount of obliging trouble which may be conceived, took for me in the Melbourne Zoological Gardens observations on the temperature of the emu. These are the lowest records of bird temperatures of which I know. They averaged 39·5°, while all the birds above the Ratitæ are invariably over 40°. The temperature of thirty-six fowls, taken quietly by night from their perches, averaged 41° exactly, while that of twelve, lifted from the nests in which they were brooding, was 41·4°. Numbers of fowls caught while roaming about averaged 41·3°, but these of course were always warmed up previously by a little violent exercise. Turkeys stand about the same level; ducks are stated, on good authority, to be lower; but I have found for these birds, from a fairly large number of observations, an average of 42·1°. The temperatures of birds of the more intelligent orders is generally somewhat higher. If we exclude the birds of prey, we might say that in all orders above the anseres, grallæ and gallinæ the temperature ranges over 42°. It would be a matter of interest to secure some observations of the temperature of the apteryx, in order to determine whether the lowest of birds shows by its body warmth in some degree the same reptilian affinity which the monotremes exhibit. In that case there would be reason to believe that the rest of the Ratitæ would correspond closely to the Marsupials, being a connecting link, but much closer to the higher forms than to the lower.

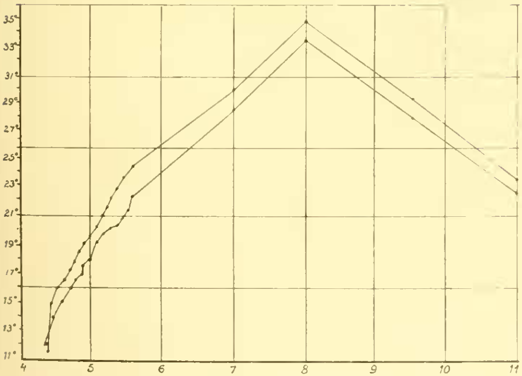
In a very general way, and not forgetting numerous limitations and contradictions, it may be said that bodily activity depends on body temperatures, that creatures such as insects, and reptiles are active only when warmed up from without, but become torpid with decreasing temperature. The type in which activity is generally habitual, maintains its own body temperature. This is



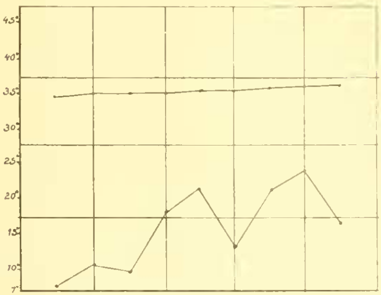
To show concomitance of temperatures of Lizards and Water
Upper Line Temperature of Water (deg. Cent)
Lower Line Temperature of Lizards



To show want of concomitance in Temperatures
of Echidna and air
Upper Line Echidna
Lower Line Air.



With more rapid heating



To show want of concomitance in Temperatures
of Koala and Air
Upper Line Koala
Lower Line Air.